Structural development of balsam-fir dominated stands following a spruce budworm outbreak

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Tiivistelmä/Referat – Abstract

The boreal forest is one of the largest biomes in the world, maintaining natural disturbances such as forest fires and insect outbreaks, still occurring widely at their full scale, frequencies and patterns. However, the knowledge of natural forest dynamics, disturbance factors other than fire and post-disturbance development is still inadequate; this is partly due to the lack of accurate, repetitive measurements with adequate temporal resolution.

The aim of this study was to examine the structural change and development of natural, *Abies balsamea* (L.) Mill. dominated forest stands following an insect outbreak of late-1970s to early 1980s. The focus was on annual tree basal area and species composition change at the stand level during the recent decades. The post-disturbance stand development was studied to see whether the stands were following the development model of steady state and quasi-equilibrium. Additionally, the size and age structure of the stands were studied. The objectives were achieved by using dendrochronological methods with tree-ring analyses, in which the forest characteristics were reconstructed at an annual resolution. The study was carried out in the province of Quebec in Eastern Canada, in the North Shore region (Côte-Nord) of St. Lawrence River. Nine sites of a size of 32 m x 32 m were chosen for data collection.

The results showed that the tree species composition of the studied stands had clearly changed from the pre-episode to the current state: the composition of *A.balsamea*, *Picea mariana* (Mill.) BSP and *Betula papyrifera* Marsh. in 1975 had changed towards the abundance of *A. balsamea*, with notably less of *P. mariana* and *B. papyrifera* in 2013. Particularly *B. papyrifera* seems to disappearing from the studied stands. On average, the shape of the live tree diameter distribution for the whole study area was close to a reverse-J, whereas the dead tree diameter distribution resembled rotated sigmoid, with a plateau in the middle. The trees were of all age, mean age for live *A. balsamea*, *P. mariana* and *B. papyrifera* trees was 91 years (SD ± 32 years), 135 years (SD ± 48 years) and 180 years (SD ± 24 years), respectively.

The examination of the development of total basal area showed apparent changes during the four decades from 1975 to 2013. The average stand development of total basal area for the whole study area was modest decline after a dramatic post-outbreak drop: the basal area was 33.8 m^2 ha^{-1} (SD ± 4.5 m^2 ha^{-1}) in 1975 and 20.7 m^2 ha^{-1} (SD ± 6.0 m^2 ha^{-1}) in 2013. Stands showed different types of development: for some of the stands basal area had dropped throughout the observation period, for some the total basal area had started to recover after a decline, and some stands had fairly stable development throughout the observation period. The development of basal area in the past fifteen years has been negative in over half of the studied stands; it seems that the stands are not following the expected post-disturbance development, where the biomass of the forest recovers to the pre-outbreak level and over it, at these time scales of 30-years of observation.

Results suggest that the studied forest stands have reached a state where the basal area is yet to be recovered from the decline following the spruce budworm outbreak in the late-1970s to early 1980s. There is a new, on-going defoliation of spruce budworm – that already has heavily affected particularly *A. balsamea* – in the study area, and therefore the basal area of the forest stands might be expected to furthermore decline in the future.

Avainsanat – Nyckelord – Keywords
Boreal forest, natural disturbance, dendrochronology, forest structure, basal area, tree species composition, spruce budworm outbreak, Abies balsamea, Picea mariana

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Tiivistelmä/Referat – Abstract

Erilaiset häiriöt, kuten metsäpalot ja hyönteisepidemiat, ovat keskeinen osa boreaalisen metsävyöhykkeen luonnonmetsien dynamiikkaa. Tiedot luonnonmetsien dynamiikasta, muista häiriötekijöistä kuin metsäpaloista ja häiriönjälkeisestä kehityksestä ovat kuitenkin puutteellisia, eikä aiempien tutkimusten ajallinen resoluutio ole ollut riittävä yksittäisten vuosien aikana tapahtuneen kehityksen tarkasteluun.

Tämän tutkimuksen tavoitteena oli selvittää, miten luonnontilaisten palsamipihdan (*Abies balsamea* L. Mill.) vallitsevien metsiköiden pohjapinta-ala ja puulajisuhteet ovat kehittyneet 1970-1980-lukujen taitteen hyönteistuhoa seuranneina vuosikymmeninä. Metsiköiden kehitystä verrattiin olemassa oleviin vanhojen metsien häiriönjälkeistä kehitystä kuvaaviin malleihin. Kehitystä tutkittiin vuoden resoluutiolla, rekonstruoimalla puuston tunnuksia dendroekologisin menetelmin. Tutkimus toteutettiin Quebecin provinssissa itäisessä Kanadassa, Saint Lawrence-joen pohjoisrannikolla. Tutkimuksen aineisto kerättiin yhdeksältä 32 x 32 m:n koealalta.

Tulosten perusteella metsiköiden nykyinen puulajikoostumus on selvästi muuttunut häiriötä edeltäneestä ajasta: vuonna 1975 metsiköiden puulajikoostumus rakentui pääasiallisesti palsamipihdasta, mustakuusesta (*Picea mariana* Mill. BSP) ja paperikoivusta (*Betula papyrifera* Marsh.), joista kaksi jälkimmäistä olivat huomattavasti pienemmässä roolissa vuoden 2013 puulajikoostumuksessa. Erityisesti paperikoivu vaikutti olevan häviämässä metsiköiden nykyisestä puulajikoostumuksesta. Tutkimuksessa tarkasteltiin myös metsiköiden läpimittajakaumaa ja ikärakennetta. Koko tutkimusalueen keskimääräinen elävien puiden läpimittajakauma muistutti käänteistä J-käyrää, toisin kuin kuolleilla puilla, joiden keskimääräinen läpimittajakauma oli lähempänä käänteistä sigmoidia. Metsiköiden puusto oli eri-ikäisrakenteista, elävien palsamipihtojen, mustakuusien ja paperikoivujen keski-ikä oli 91 (SD ± 32 vuotta), 135 (SD ± 48 vuotta) ja 180 vuotta (SD ± 24 vuotta).

Metsiköiden pohjapinta-alan havaittiin myös muuttuneen tarkastelujakson aikana. Tutkimusalueiden pohjapinta-ala laski keskimäärin 10-20 m^2 ha^{-1} tarkastelujakson aikana. Vuonna 1975 metsiköiden keskimääräinen pohjapinta-ala oli 33.8 m^2 ha^{-1} (SD ± 4.5 m^2 ha^{-1}), kun vuonna 2013 se oli keskimäärin 20.7 m^2 ha^{-1} (SD ± 6.0 m^2 ha^{-1}). Dramaattisin pudotus tapahtui välittömästi häiriön jälkeen. Metsiköiden välinen kehitys erosi kuitenkin toisistaan: osalla metsiköistä pohjapinta-ala laski koko tarkastelujakson ajan, osalla näkyi lievää palautumista pudotuksen jälkeen ja osalla oli melko tasaista kehitystä läpi koko tarkastelujakson. Viimeisen viidentoista vuoden aikana metsiköiden pohjapinta-alan kehitys on ollut negatiivista yli puolella metsiköistä; näiden tuloksien perusteella metsiköt eivät ole seuranneet tutkimuksen tarkastelujaksolla vanhojen metsien häiriönjälkeistä kehitystä kuvaavaa mallia, jossa metsikön biomassa palautuu häiriötä edeltävälle tasolle ja sen yli.

Tuloksien perusteella voidaan sanoa, että tutkittujen metsiköiden rakenne on tilassa, jossa metsiköiden pohjapinta-ala ei ole vielä palautunut 1970-1980-lukujen taitteen kuusikääriäistuhoa seuranneesta romahduksesta. Tutkimusalueella on todettu olevan uusi käynnissä oleva kuusikääriäistuho, joka on ehtinyt jo aiheuttaa eritoten palsamipihdan harsuuntumista. Näin ollen metsiköiden pohjapinta-alan voidaan olettaa laskevan entisestään myös tulevaisuudessa.

Avainsanat – Nyckelord – Keywords
Boreaalinen metsä, luonnontilainen häiriö, dendrokronologia, metsikön rakenne, pohjapinta-ala, puulajikoostumus, kuusikääriäistuho, *Abies balsamea*, *Picea mariana*

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Contents

1 INTRODUCTION

1.1 Disturbance dynamics in boreal forests

The boreal forest is one of the largest biomes in the world, containing over twenty thousand identified species of flora and fauna and preserving a significant amount of global carbon stocks (Ruckstuhl et al. 2008, Bradshaw et al. 2009). Natural disturbances such as forest fires and insect outbreaks still widely exist in the boreal forest zone, occurring extensively at their full scale, frequencies and patterns (Ruckstuhl et al. 2008).

According to Pickett and White (1985), disturbance can be described as "any relatively discrete event in time that disrupts ecosystems, community or population structure and changes resources, substrate availability, or the physical environment". Disturbance and succession are the two major processes that maintain the habitat heterogeneity at different scales and allow the continuous renewal of natural boreal forests (Kuuluvainen 2002). Disturbances in forest ecosystem have a crucial part in determining the species composition, structure and processes (McCarthy 2001).

Disturbances can be roughly divided into autogenic disturbances that originate from within the forest ecosystem and allogenic disturbances that originate from outside the forest ecosystem (Kuuluvainen 2002, Rouvinen et al. 2002). Harmon et al. (1986) names wind, insects, fire, diseases, tree competition and suppression as the main mortality agents of trees. Pathogenic fungi and mortality due to tree competition are examples of autogenic disturbances, and insect outbreaks, strong local winds and heavy snow or ice storms are examples of allogenic disturbances (Franklin et al. 1987, Kuuluvainen 2002). In many cases, tree mortality is a combination of complicated occurrences containing multiple disturbance agents: for example, decaying fungi might be the primary reason for tree mortality, as it weakens the tree and predisposes it to stem breakage made by some other, secondary mortality agent, such as heavy snow or wind (Franklin et al. 1987).

When discussing disturbance agents, the subject of forest fires is bound to come up. Fires are important drivers of disturbance in natural boreal forests (Zackrisson 1977).

However, their significance is perhaps overly emphasized at the expense of other types of disturbances (Kuuluvainen 2002). The moist maritime climate in areas of North America and Northern Europe is one of the reasons the occurrence of fire is not uniform over the boreal zone (Granström 2001, Bouchard et al. 2008). The generalization, that boreal forests are controlled by severe disturbance, such as forest fire, resulting to total stand replacement and domination of even-aged stand successions, has been proven to be oversimplification (Kuuluvainen 2009). A review concerning natural forest dynamics of boreal Fennoscandia (Kuuluvainen and Aakala 2011) demonstrated that unmanaged forests are characterized by diverse and complex dynamics, including as well stand-replacing and partial disturbances as tree mortality at intermediate (i.e. patch dynamics) and fine (i.e. gap dynamics) scales.

In areas of the boreal forest where the fire return intervals are long, the significance of other types of disturbances increases. As trees senescence and die of age in between or in the lack of severe disturbances, changes in the forest structure and species composition can become driven by gap dynamics (Oliver and Larson 1996). Gap dynamics is characterized by disturbances operating at the small scale of the mature forest canopy, affecting individual trees to small group of trees (McCarthy 2001). As in the case of large-scale disturbances, gap disturbances are driven by both autogenic and allogenic factors (Oliver and Larson 1996). Gap disturbances have less dramatic effect on forest stand than large-scale disturbances, but even individual tree mortality can affect tree population structure and allocation of resources considerably (Franklin et al. 1987).

The fluctuation of live and dead biomass is a part of the dynamics of both gap- and large-scale disturbances. According to a model by Bormann and Likens (1979), after a disturbance the biomass of the forest undergoes four phases of development: in the first phase the biomass declines as the ecosystem goes through drastic changes due to disrupt of structure, in the second phase biomass steadily increases to a maximum as the ecosystem storages biomass, in the third phase the biomass erratically declines as the previously dominant old even-aged trees begin to die, and finally, in the fourth phase the biomass somewhat stabilizes and irregularly oscillates around some mean biomass (Fig. 1). The final phase is called shifting-mosaic steady state (Bormann and Likens 1979). The more recently presented idea of quasi-equilibrium in old-growth forests holds the same idea of slow, constant cycling through changes in biomass and species

composition and function; in quasi-equilibrium, forest reaches relative structural and compositional equilibrium with relatively small and constant disturbances (Shugart 1984, Caron et al. 2009). Quasi-equilibrium conditions have been connected with tropical and temperate forests, but there are studies that suggest such conditions can occur in old-growth boreal forests as well (Caron et al. 2009).

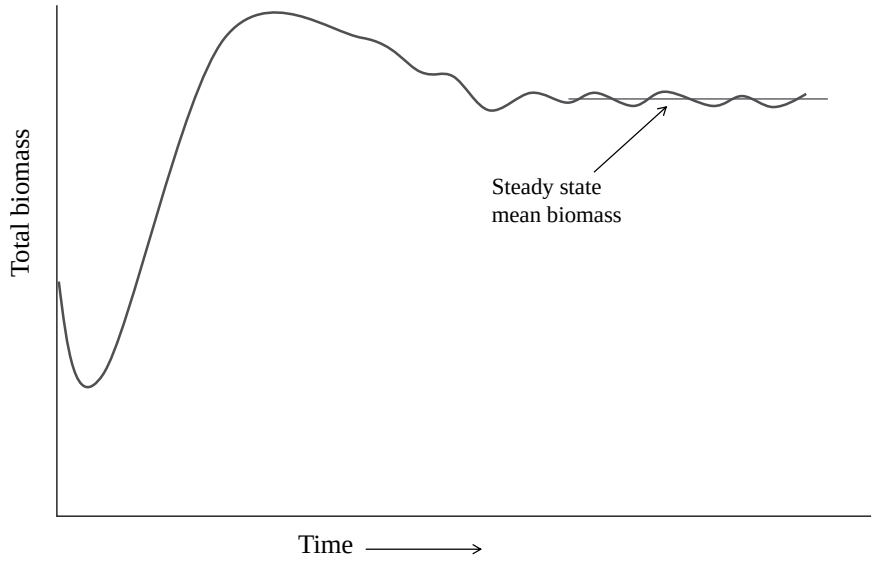

Fig. 1. Shifting mosaic of steady state model of forest ecosystem development following a disturbance based on total biomass (living plus dead) accumulation, in which biomass rises to a peak, loses biomass, and then irregularly oscillates around some mean through time (Bormann and Likens 1979).

1.2 Disturbance dynamics in the North Shore region

The North Shore region of Quebec, Canada, is an example of a boreal region where natural forest fires occur infrequently. The fire return interval has been shown to vary throughout the North Shore, often reaching a time period longer than the life cycle of the post-fire tree species (Pham et al. 2004, Bouchard et al. 2008, Gauthier et al. 2010). Thus gap disturbances play a considerable role in the region's forest dynamics (De Grandpré et al. 2009).

In the western part of the North Shore, a major insect pest Eastern spruce budworm (*Choristoneura fumiferana* Clem.), a species of moth, causes serious damage and mortality to coniferous stands (De Grandpré et al. 2009). Spruce budworm defoliates

primarily *Abies balsamea* (L.) Mill., along with *Picea glauca* (Moench) Voss., *Picea rubens* Sarg., and *Picea mariana* (Mill.) BSP (Bouchard et al. 2005, Bouchard and Auger 2014). Within the past 450 years, spruce budworm outbreaks seemed to occur in conifer dominated forests of southeastern Quebec in cycles, two or three times in a century (Boulanger and Arseneault 2004). The infestations are linked to the structure of tree stands, and the outbreak is most likely to occur in areas with abundant matured *A. balsamea* stands (Blais 1983). The larvae of the spruce budworm usually feeds on the current-year shoots of the host trees, but in the absence of new shoots the larvae can feed on older foliage as well (Royama 1984). When occurring at high densities, spruce budworm causes extensive damage to conifer stands by reducing the growth of the trees, even resulting in tree mortality of entire stands (Royama 1984, Bouchard et al. 2006). During infestation the population density of the insect remains high for several years, until it usually settles after destruction of considerable amount of firs and lesser amount of spruces (Blais 1983).

During the 20th century three spruce budworm outbreaks have been recorded in Eastern Canada: in 1910-1920, 1940-1950 and 1970-1980 (Blais 1983). In the North Shore region the first and the last outbreak of the 20th century have been reported to cause varying degrees of defoliation, the last one of late-1970s to early 1980s causing the highest damage (De Grandpré et al. 2009); according to Blais (1983), it affected a forest area of more than 90 000 km^2. Depending on the species composition before the outbreak and the mortality of host and non-host species following the outbreak, it seems that the outbreak of late-1970s to early 1980s has had different sorts of effect on stand regeneration patterns for different stand types: total stand replacement in *A. balsamea* dominated stands of high mortality, multi-level canopy structures in mixed boreal stands where mortality has been partial, and gap-like dynamics in mixed hardwood stands with limited number of host species (Bouchard et al. 2005). The provincial ministry of natural resources of Quebec, Canada, has recently reported of on-going spruce budworm defoliations, which has been appearing across the province during the period 2003-2011 (QMNFR, cited in Bouchard and Auger 2014).

There are a few other disturbance agents that are typical for the North Shore region. In the eastern part of the North Shore, the hemlock looper (*Lambdina fiscellaria fiscellaria* Guen.) is the nuisance of the area's forests (De Grandpré et al. 2009). Wind damage occurs periodically in the area, causing both partial and total stand mortality (Bouchard

et al. 2009, Girard et al. 2014). It seems that *A. balsamea* is prone to treefall in this type of disturbance, but also that partial windthrow creates opportunities for growth release of pre-established *A. balsamea* (Girard et al. 2014). Besides creating smaller gaps, other disturbances such as ice storms and heavy, wet snowstorms can cause significant damage in the area's forests (De Grandpré et al. 2009).

1.3 Objectives

Although disturbance dynamics play a key role in natural forests, knowledge of natural forest dynamics, disturbance events other than fire and post-disturbance development of natural forests is still limited. The aim of this study was to examine the structural change and development of natural, *A. balsamea* dominated forest stands following an insect outbreak. Previous studies have documented such change with interpretation of aerial photographs (e.g. Gauthier et al. 2010). A weakness of these kinds of studies is the poor temporal resolution they provide; to understand long-term post-disturbance development of forest stands, inter-annual development is required to distinguish all the annual changes in stand structure and dynamics. However, annually measured permanent plots are rare, and in this case, missing. To counter the lack of permanent measurement plots, an option is to use "biological archives" such as tree rings; trees can be considered as instruments for environmental monitoring, and tree-ring research provides a possibility to reach back to past conditions and structure of studied forest stands (Speer 2010).

The objective was to examine how annual tree basal area and species composition have changed at the stand level during the recent decades. This was achieved by using dendrochronological methods with tree-ring analyses, in which the forest characteristics were reconstructed at an annual resolution. The focus was on *A. balsamea* dominated stands, which are prone to insect outbreaks. There were three time episodes in this study: during the outbreak (1975), after the outbreak (1980->) and present time (2013). It is expected that the basal area initially declines after the outbreak, but post-outbreak development is unknown. Considering that there is a new outbreak occurring in the North Shore region, a relevant question is how the stand development relates to the

existing model of steady state and quasi-equilibrium of old-growth forest stand development.

Here, I ask the following questions:

1) How has stand basal area and structure changed in the recent decades, following the spruce budworm outbreak of late-1970s to early 1980s?
2) How the change varies among studied stands?
3) Is this development consistent with the steady state/quasi equilibrium model of stand development of old-growth forests?

2 MATERIALS AND METHODS

2.1 Study area

The study was carried out in the province of Quebec in Eastern Canada, in the North Shore region (Côte-Nord) of St. Lawrence River (49.5°-50.0° N, 67.5°-69.0° W). The area belongs to the *Abies balsamea-Betula papyrifera* bioclimatic subdomain (Robitaille and Saucier 1998, cited in Pham et al. 2004).

Natural forests of the area are mainly dominated by *A. balsamea* and *P. mariana*, mixed with *P. glauca* and individual deciduous trees (*Betula papyrifera* Marsh. and *Populus tremuloides* Michx). About 74 % of the North Shore's forest areas are dominated by conifers, 10 % is regenerating, and remaining area is either dominated by mixedwood (13 %) or hardwood (3 %) stands (MRNFP 2004, cited in De Grandpré et al. 2009). There is only a few tree species present in the region, but despite this there is significant variation in the structure and composition of the areas forests (Gauthier et al. 2010).

Climate in the North Shore is cold and maritime: mean annual temperatures fluctuate between -2.5 and 0.0°C, and annual precipitation varies between 1100 and 1300 mm, 35

% of which falls as snow (Robitaille & Saucier 1998, cited in Pham et al. 2004). Forestry has been part of the region's history for long (especially in the southern parts of the North Shore with more extensive road network), but various forest stands are still unmanaged and in their natural state, suitable for studies of natural forest dynamics (Bouchard et al. 2008). Although forest fires that cover extensive areas are rare in the North Shore region, some fires have been recorded during the 20th century (De Grandpré et al. 2009). However, the natural mean fire return interval of the North Shore is comparatively long, varying from 200 years to over 500 years, and the last recorded forest fire in the study area was over 200 years ago, in 1810 (Bouchard et al. 2008).

2.2 Data collection and handling

The area, that was accessible but spared from loggings and mostly dominated by *A. balsamea*, was selected from database provided by the Quebec Ministry of Natural Resources (Québec Ministère de l'Énergie et des Ressources naturelles). A 2 km x 2 km grid was placed over the area and divided to quadrants; of each quadrant three sites were randomly picked, and nine sites of a size of 32 m x 32 m were chosen for data collection. That the stands were accessible means that they were within an area that was being logged, and the reason for saving these areas from logging was unknown.

The trees were mapped in each site using FieldMap measuring system (IFER LTD, Czech Republic), which consisted of an electronic compass and a laser rangefinder, paired with handheld computer running the FieldMap measurement software. All live trees with a diameter at breast height (DBH, breast height meaning 1.3 m) equal to or greater than 10 cm were included in the mapping. DBH and tree height were recorded for each tree along with tree species; along with *A. balsamea* and *P. mariana*, some of the sites might have contained individual *P. glauca* trees, but they were not separated from *P. mariana*. Any top damage such as broken crown was also noted, and the defoliation level of each tree caused for example by the on-going spruce budworm outbreak was visually classified on a scale of 1-6: 1 = <1% of needles defoliated, 2 = 1-25%, 3 = 25-50%, 4 = 50-75%, 5 = >75% defoliated. Each tree was also categorized by its crown position to one of the four following classes, which describe the degree of

dominance and suppression of the trees: dominant, co-dominant, intermediate or overtopped (Kraft 1884, cited in Oliver and Larson 1996).

In addition to live trees, all dead trees with DBH equal to or greater than 10 cm were mapped from each site. DBH and height were recorded, and the mode of mortality noted: the tree was classified as down woody debris (DWD) if it was less than 1.3 meters in height measured from the root collar (meaning a fallen dead tree), a snag (standing tree) if it was over 1.3 meters in height, intact if the standing dead tree had no noticeable damage in the top, and uprooted if it had fallen down with its roots lifted. If the dead tree was standing and intact, the height was usually measured from the tree base to the top with the laser rangefinder, and if it was a snag, the height was visually evaluated to an accuracy of 0.10 meters. The decay class was determined for each dead tree on a scale of 1-6, where 1 is recently dead trees and 6 advanced decomposed trees covered with vegetation (according to Aakala 2010; Table 1).

Table 1. Decay classes (Aakala 2010). Snag = standing dead tree, DWD = down woody debris.

Class	Type	Description
1: Recently dead	Snag or DWD	Small branches with at least some foliage still attached.
2: Early	Snag or DWD	Foliage absent. Small twigs still present.
3: Early-intermediate	Snag or DWD	Smallest twigs absent, most of the largest branches still present.
4: Intermediate	Snag	Only a few of the largest branches possibly present, snapped.
	DWD	Only a few of the largest branches possibly present, stem shape round.
5: Advanced	Snag	Less than 2 m high, highly deteriorated. Branches gone.
	DWD	No branches, loss of log shape.
6: Covered	DWD	Totally covered with ground vegetation.

All live trees included in the mapping were cored with a standard increment borer for tree-ring measurements. Each tree was cored at the breast height (1.3 meters). This provided us with a sample of tree core, showing all the annual growth rings from the recruitment year of the tree to the present year of the coring. Recruitment year is the

year that saplings are added to the tree population, and thus have survived the initial states of succession. Shade-tolerant trees, such as *A. balsamea*, have the ability to persist suppressed in the sub-canopy for years and to escape the initial competition of resources started by a disturbance (Canham 1985). Dead trees were also cored if possible, as it was usually in the case of recently killed trees, i.e. decay class 1 (Table 1). If the outer parts of the stem were too decayed for coring, samples were extracted with a chainsaw.

In the laboratory, all the cores from live trees were glued with water-soluble white glue to a prefabricated wooden mount, dried, and sanded to fine grit using progressively finer sandpaper, to 600 grit for conifers and 1000 grit for deciduous trees. The purpose was to obtain the annual rings as clear and visible as possible; dendrochronology and ring identification relies on the visual observation of single cells to determine the ring boundaries (Speer 2010). The sample discs from the dead trees were also dried and sanded to enable the analysis of the annual rings; fragile discs were immersed in a glue solution for 1-2 weeks before drying and sanding (as in Krusic and Hornbeck 1989, but in normal air pressure).

2.3 Tree ring measurements

2.3.1 The principles of dendrochronology

Dendrochronology explores different occurrences through time that are recorded in tree-ring structure, or that can be otherwise dated by tree rings (Speer 2010); part of the dendrochronology is dendroecology, focusing on the interactions between tree growth and environment.

Conifer and deciduous trees in seasonal climate produce one ring per year: this so called annual ring can be divided into earlywood and latewood according to its formation time (Speer 2010). Trees produce earlywood usually in spring and early summer, and latewood in the late summer. Earlywood cells have large lumen relative to the cell walls whereas latewood cells have more compact lumen relative to the cell walls and therefore appear darker than earlywood cells (Speer 2010). The ring boundaries of

conifers can consequently be detected by examining the size and cell wall thickness of the tracheids, which are the tubelike cells of the wood (Speer 2010). Tracheids can be detected for example with a microscope. Deciduous trees have more complex wood structure than conifers, but ring boundaries can be defined by the size of the fibers, size of the lumen and thickness of the cell walls (Speer 2010).

Usually trees produce wide, easily detectable annual rings during times of good environmental conditions (reflecting the fast growth of trees), but in stressful years, e.g. in times of drought or during insect attacks, the growth hormone production of trees is limited, which can lead to narrow or missing annual rings (Speer 2010). In order to determine the exact dates of the annual rings, the false and absent rings must be detected. The fundamental idea behind crossdating is that certain kind of factors limiting the tree growth at the scale of an individual tree ring leads to a narrow annual ring width, which is then repeated in the majority of trees growing in similar environmental conditions (Speer 2010). Hence the narrow annual rings are important recorders of growth limiting factors, and crossdating is based on the visual observation and recording of narrow or otherwise differing annual rings, and matching the ring width patterns between separate trees.

Here the goal of crossdating was to 1) place verified calendar years to each annual ring of the live tree samples so that the biomass change could be examined, and to 2) date the timing of death and the measurements of the dead tree samples. After crossdating the samples from live and dead trees, the next step was to measure the rings widths with the WinDENDRO software (Regent Instruments Inc. 2015) and to verify the visual crossdating observations and the measurements with the computer program COFECHA (Holmes 1983).

2.3.2 Crossdating

The dating began from the determination of the so called marker rings: rings that were particularly narrow compared to other annual rings, or had other identifiable characters, were recorded using methods created by Yamaguchi (1991). Determining marker rings was started from the outermost bark-side ring of the core sample, which is the last year the tree has grown so far and is usually the year of the sampling.

When comparing the marker rings from individual trees, it was possible to create a list of composite marker rings for each sampled tree species (Table 2): if a ring was consistently narrow (or otherwise differing, such as dark or remarkably wide) among the samples, it was included in the composite marker ring list. After this the other samples were quickly dated with the aid of composite marker rings: when all the samples had the same marker rings at the same year, it was possible to be sure that the annual rings of the cores were correctly dated.

Table 2. List of composite marker rings for *Abies balsamea* and *Picea mariana*. Notes: n = narrow ring, w = wide ring, D = dark colored ring, vn = very narrow ring, absent = ring missing.

Abies balsamea		Picea mariana	
Date	Notes	Date	Notes
1996	n	2009	n
1994	n	1999	w
1984	n	1982	w
1983	w	1979	vn/absent
1980	wD	1978	n/vn
1979	vn/absent	1961	w
1978	vn/absent	1943	n
1968	n	1938	n
1962	n	1935	w
1961	w	1929	n
1960	n	1926	n
1956	n	1925	n
1950	n	1921	n
1947	n	1900	w
1942	wD	1897	w
1938	n	1893	n
1917	n	1890	n

Once a list of marker rings from live trees was compiled, the dead trees could be crossdated. In the case of boreal forests, there is often sufficient variation in the growth of the trees so that also the dead trees could be reliably dated with the techniques by Yamaguchi (1991). The dead tree samples differed from the live tree samples by that the year of the outermost ring, which is the date of the tree's death, was unknown. When the occurrence of marker rings on the dead tree samples were compared against the occurrence of live tree marker rings, the recruitment years and the years of the outermost ring of dead trees were also possible to date correctly.

2.3.3 Measurements and verification

After visual crossdating of tree-rings, software WinDENDRO (Regent Instruments Inc. 2015) was used to measure the tree-ring widths. WinDENDRO uses digital images of the tree core samples to create "paths" of measurement: WinDENDRO was indicated manually where to measure rings in the image. Paths were traced with a perpendicular trajectory to each ring boundary, proceeding from the inner pithside rings to the barkside rings. After a path was created, rings were automatically detected by WinDENDRO. The path had to be checked for the presence of false or absent rings, or misinterpretations of WinDENDRO; rings were deleted and added if necessary, the previously made marker ring list of visual observation as a guide for placing the rings.

The dating and measurement check was done with the program COFECHA, a command-line driven program in DOS (Holmes 1983). COFECHA was created to enhance data quality control and to serve as a "second check" on the visual dating of tree-rings (Holmes 1983). It provides a statistical match between segments of each core and the reference chronology, i.e. master chronology, built from the previously validated measurements that are entered into the program (Speer 2010). This master chronology was constructed of visually crossdated samples of live trees. If necessary, the measurements were modified in WinDENDRO according to the suggestions made by COFECHA, then checked again with COFECHA, and finally approved. As proceeding, all the new validated tree-ring measurements were added in the master chronology used in COFECHA as reference measurements. Deciduous tree samples

differed from conifers in that there were considerably less *B. papyrifera* to build an adequate master chronology to serve as a reference in COFECHA, and therefore the results for *B. papyrifera* are indicative.

After COFECHA analysis, additional information from samples was gathered for data analyses, including whether the sample had its barkside rings attached, whether there was an actual pith or not and how many millimeters to pith there was. When a core was missing pith (for example due to mistargeted coring or heart-rott), a pith indicator was used. A pith indicator is a series of concentric semi-circles (applequist pith locator in Applequist 1958).The proper set was chosen based on the size of the innermost rings on the core, and the curvature of the rings was then matched up to the curvature of the pith indicator; the number and millimeters of rings that were missing to the pith were counted and written down. The result was a rough estimate for the actual pith date, but according to Speer (2010), it is a better option than simply using the inner ring date.

2.4 Data analysis

The basal area of a forest stand is the sum of cross-sectional areas of individual trees measured at breast height (1.3 m) in meters squared per hectare. The basal area of the trees was calculated after the area of a circle, even though in reality the tree shape may be often closer to an oval than a perfect circle. In the field the trees were cored radially from random directions, in which case the coring was done both in the "long" and "short" side of the oval shaped tree. It was assumed that this provided correct basal area as an average for the whole stand.

The annual basal area of an individual tree was calculated as the difference in area between two circles, i.e. between two annual basal areas, at year *t* and at year *t*-1, *r* as the tree's radius length:

$$A = \pi * {r_t}^2 - \pi * {r_{t-1}}^2$$

The 2013 basal area was obtained from the field measurements:

$$\pi * \left(\frac{DBH}{2}\right)^2$$

The other annual basal areas were derived from the ring-width measurements. The calculations were made from bark to pith, and the share of the bark was reduced from the calculations (according to Li and Weiskittel 2011 for conifer trees and Weiskittel & Li 2012 for deciduous trees). The annual basal area for each site was obtained by summing the basal area of individual trees (both live trees and dead trees, which were live in the year in question) for each year. For samples lacking some parts of the core or annual rings (for example due to splitting of the core or mishandling), the growth was calculated with a simple model that predicted annual ring widths as a function of species and diameter, based on the data from intact samples.

The change of stand basal area was obtained by calculating the annual basal area for each site from 1975 to 2013. The site-specific differences were obtained by comparing the development of stand basal area between each site. To study the structural change of the sites, tree species composition and diameter distribution per site and age structure per tree species were examined. Dead trees had some uncertainties, as trees belonging in the decay class 4 of intermediate stage of decay, 5 of advanced stage of decay, and 6 of covered dead trees (Table 1), included trees that were impossible to date due to advanced decomposition of wood; the dating is not possible if the outermost growth rings have disappeared or decayed unrecognizable. Undated trees in the decay class 6, which were completely covered under ground vegetation in the forest and were highly decomposed, were assumed to have died before the outbreak of late-1970s to early 1980s, and decay classes 4 and 5 were assumed to have died during the outbreak. This assumption relies on the decay class transition models by Aakala et al. (2008) for standing dead trees, which showed that decomposition rates in these forests are fairly low: an average standing dead *A. balsamea* reaches advanced stages of decay after 30-35 years, and *P. mariana* 35-40 years after death.

All the calculations were done with R, the free software environment for statistical computing and graphics (R Core Team 2013), and with the package dplR (Bunn 2008).

3 RESULTS

3.1 Current stand structure

In summer 2013, the total basal area of the sites' live trees varied between 12 and 31 m^2 ha^{-1} (Table 3). The densest tree structure and highest basal area was in site 3, with 980 trees per hectare and basal area of 30.4 m^2 ha^{-1}. Site 1 contained the lowest number of trees per hectare (600) and the lowest total basal area (12.4 m^2 ha^{-1}). On average, the total basal area of the sites was 20.7 m^2 ha^{-1} (SD ± 5.6 m^2 ha^{-1}). The mean diameter at breast height varied from 14 to 20 centimeters between sites, smallest stems in site 1 (mean DBH 15.5 cm) and biggest stems in site 5 (DBH 18.9 cm) and site 9 (DBH 19.5 cm); on average, the mean diameter at breast height of live trees was 17.2 centimeters (SD ±1.6 cm). The mean tree heights were similar on each of the sites, varying between 9 and 12 meters, sites 8 and 9 standing out with the tallest trees of over 14 meters (Table 3).

Table 3. Site characteristics (BA = basal area, DBH = diameter at breast height, SD = standard deviation).

Site	Total BA in 2013	Trees per hectare	Mean DBH (cm)	Mean height (m)
1	12.4	600	15.5	9.1
2	19.0	820	15.9	9.8
3	30.4	980	18.4	11.8
4	19.8	790	16.8	10.7
5	25.6	780	18.9	11.8
6	19.0	680	17.8	11.1
7	12.8	720	14.2	9.4
9	21.6	830	17.5	14.0
10	26.1	790	19.5	14.2
Average	20.7	776.7	17.2	11.3
SD	5.6	100.1	1.6	1.8

A major part of the live trees on the sites had suffered from defoliation to some degree (Fig. 2). Of all *A. balsamea* trees, 80 % (~ 470 trees per hectare) belonged in defoliation classes 2 and 3, meaning that *A. balsamea* had defoliated up to 50 %. *A. balsamea* had also plenty of (~ 100 trees per hectare) trees in the classes 4 and 5, meaning defoliation of needles from 50 % to over 75 %. *P. mariana* had clearly suffered less from defoliation, as most (~161 trees per hectare, 93 % of all black spruces) of its trees were defoliated less than 25 %; only few individuals (~ 4 trees per hectare) were found in classes 4 and 5 of heavier defoliation (Fig. 2).

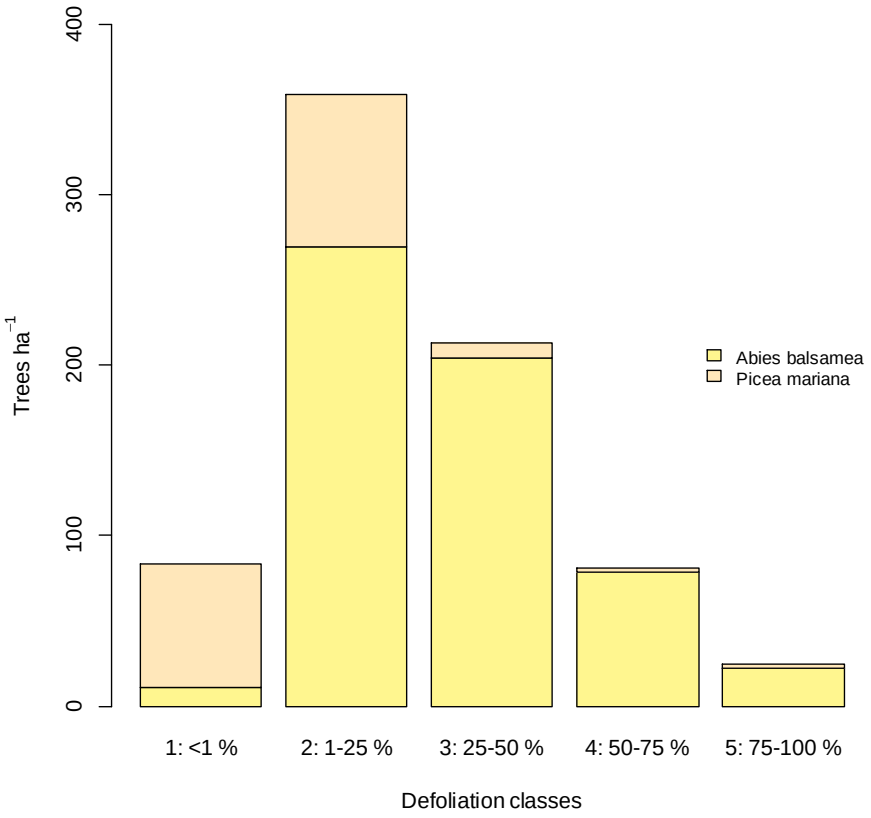

Fig. 2. The defoliation of needles of *Abies balsamea* and *Picea mariana.*

Vertical canopy structure of the live trees was classified into four canopy classes: dominant, co-dominant, intermediate and overtopped (Fig. 3). Dominant trees, which extend above the general level of the crown cover, were mostly *P. mariana* (~ 52 trees ha^{-1}, 71 % of dominant trees). *P. mariana* trees on the sites were usually co-dominant,

forming the general level of the canopy cover, whereas *A. balsamea* trees were the most common (~388 trees ha^{-1}, 66 % of all *A. balsamea*) as intermediate, trees shorter than in the two preceding classes. *B. papyrifera* trees were for the most part intermediate. Roughly 28 trees ha^{-1} of measured *A. balsamea* were overtopped, crowns completely below the general crown cover level and without direct light (Fig. 3).

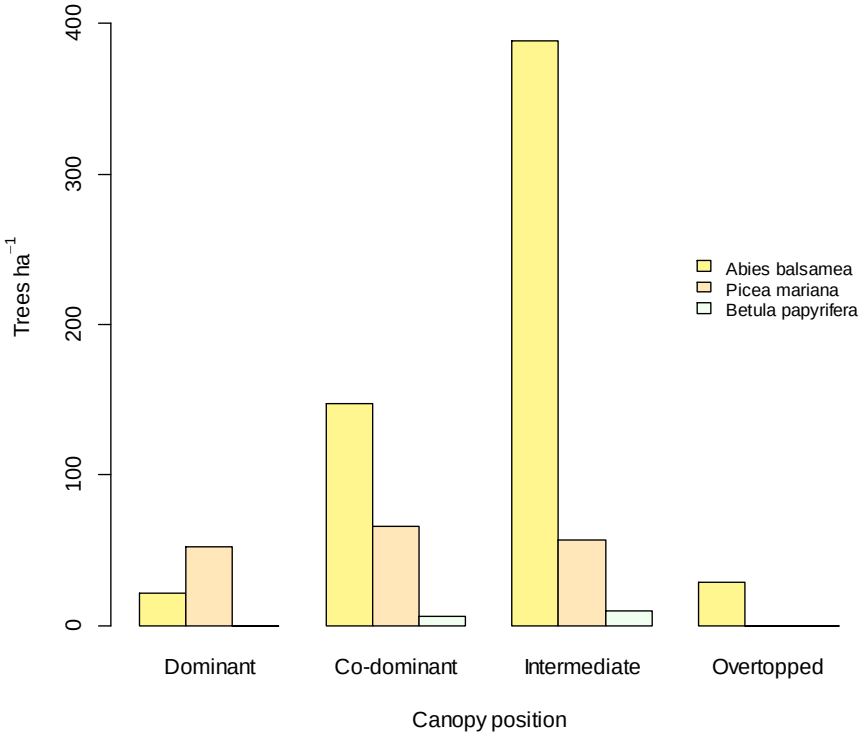

Fig. 3. Canopy structure of *Abies balsamea*, *Picea mariana* and *Betula papyrifera*.

3.2 Diameter distribution

The shape of the diameter distribution varied among the nine sites (Fig. 4). Live trees of smallest size classes (DBH < 18 cm) were the most abundant in all of the sites; site 2 and site 7 had close to 500 trees per hectare in the smallest (DBH < 14 cm) size class, whereas other sites had 200-300 trees ha^{-1} in the same size class. Tree numbers usually decreased in the larger size classes. Biggest live stems were in site 5 (DBH > 50 cm), and site 8 had the smallest range of trees in diameter (DBH < 30 cm). Compared to other sites, site 7 was lacking live trees of 22-30 cm in diameter and site 1 live trees of 26-30 cm in diameter; other sites had trees up to 34 cm in diameter. The shapes of the diameter distribution reflected the classical reverse-J fairly well in sites 1, 2, 3, 5 and 7. Site 8 and 9 had diameter distributions closer to a rotated sigmoid, with a plateau or an increase in the mid-diameter distribution range. Site 4 and site 6 were something between a reverse-J and a rotated sigmoid.

As live trees were mostly smaller in size, dead trees were more abundant in the mid-sized diameter classes (DBH > 18 cm) (Fig. 4). However, sites 2, 4 and 6 had also several dead trees in the smaller size classes (DBH < 18 cm). Site 8 had fairly constant number of dead trees up to 30 cm in diameter, whereas on most of the sites the tree numbers in the size classes first increased towards some maxima and then decreased towards the larger size classes. Biggest dead stems were in site 3 and site 6 (DBH > 50 cm).

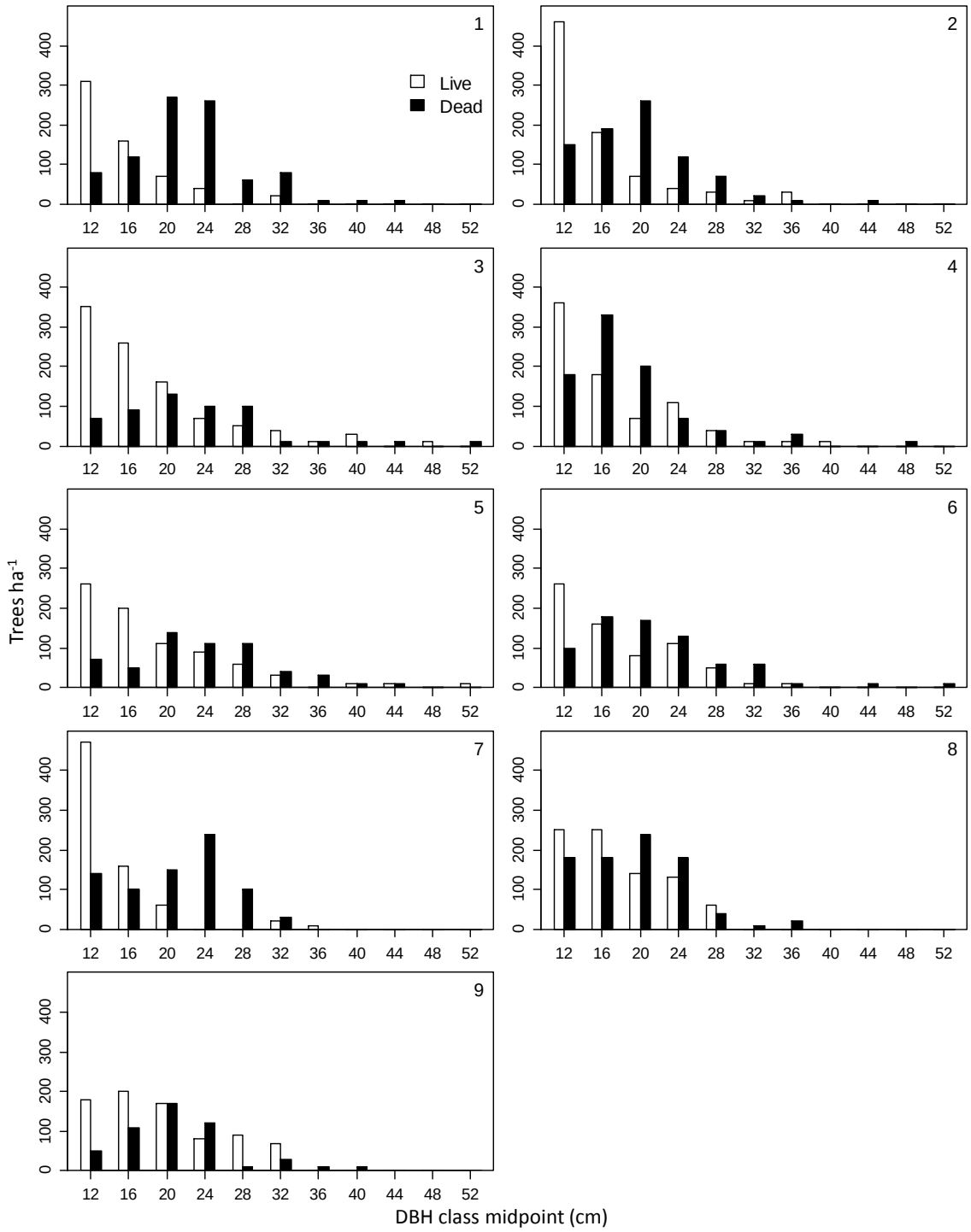

Fig. 4. Tree diameter distribution of live and dead trees for sites 1-9. Class size is 4 cm.

The shape of the live tree diameter distribution for the whole study area was close to a reverse-J (Fig. 5). Dead tree diameter distribution was closer to a rotated sigmoid. Most of the live trees were less than 18 cm in diameter (~ 517 trees ha^{-1}, 67 % of all live trees). Dead trees were greater in number in the larger (DBH > 18 cm) size classes, and

the majority of dead trees were 14-26 cm in diameter (~ 490 trees ha^{-1}, 67 % of all dead trees).

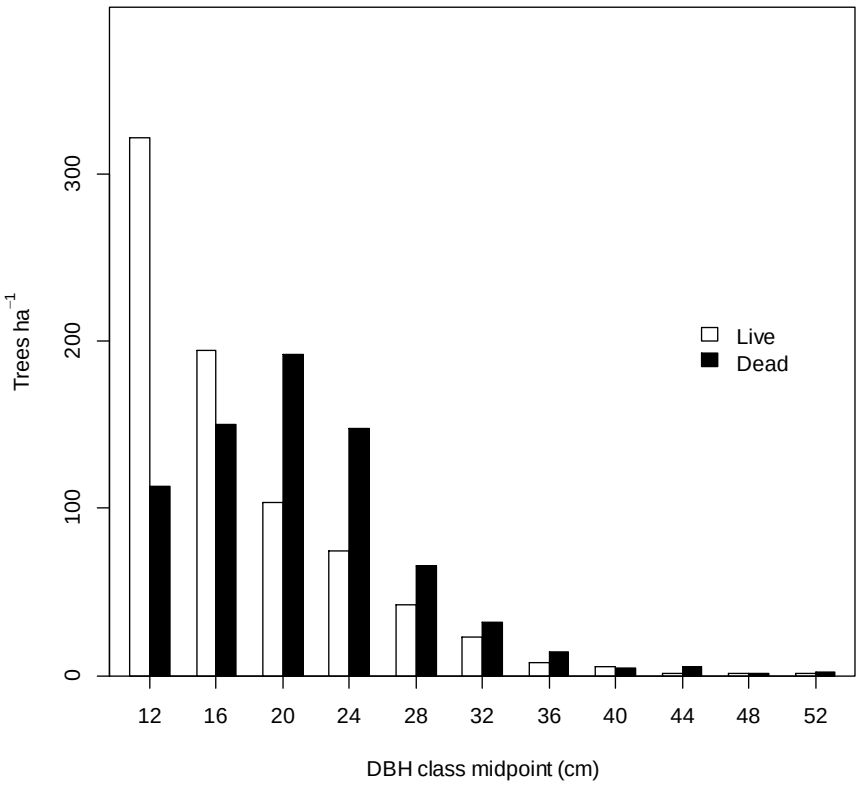

Fig. 5. Tree diameter distribution of live and dead trees for the whole study area. Class size is 4 cm.

3.3 Age structure

Tree age structure was compared per tree species for all nine sites (Appendix 1, Fig. 6-8). For *A. balsamea*, age structure was fairly evenly distributed between each site; most of the trees were recruited between 1888-1938 (Fig. 6). Site 8 did not contain much of *A. balsamea*, especially dead trees were absent. For *P. mariana*, the age distribution was somewhat different in sites which were clearly dominated by *A. balsamea* (Fig. 7); for example, site 2 had fairly even range of live and dead trees between years 1813 and 1988, whereas site 8, which contained the highest amount of *P. mariana*, had distinct age distribution in which both live and dead tree numbers increased towards the older age classes (Fig 7.). For *B. papyrifera*, sites 1-4 had fairly similar distribution: majority

of the live and dead trees had recruited between 1888 and 1813 (Appendix 1, Fig. 8). Other sites had so little of *B. papyrifera* trees that no clear distribution could be detected.

To get the differences between the three tree species more apparent, the tree age structure was also observed for all nine sites combined (Fig. 9). Trees were of all age, mean age for live *A. balsamea* trees was 91 years (SD ± 32 years), 135 years (SD ± 48 years) for *P. mariana*, and 180 years (SD ± 24 years) for *B. papyrifera*. Youngest live *A. balsamea* trees were 25-50 years old and youngest *P. mariana* trees < 25 years old, which reflects the time it took for the trees to grow to the 10 cm DBH limit. *B. papyrifera* trees were much older, youngest live trees were over 125 years old. Oldest live *P. mariana* and *B. papyrifera* trees were of same age, over 175 years old, and *A. balsamea* trees were slightly older (> 200 years old). Mean age for dead *A. balsamea* trees was 110 years (SD ± 33 years), 141 years (SD ± 36 years) for *P. mariana*, and 160 years (SD ±18 years) for *B. papyrifera* (Fig. 9). Oldest dead trees were *P. mariana* (> 225 years old).

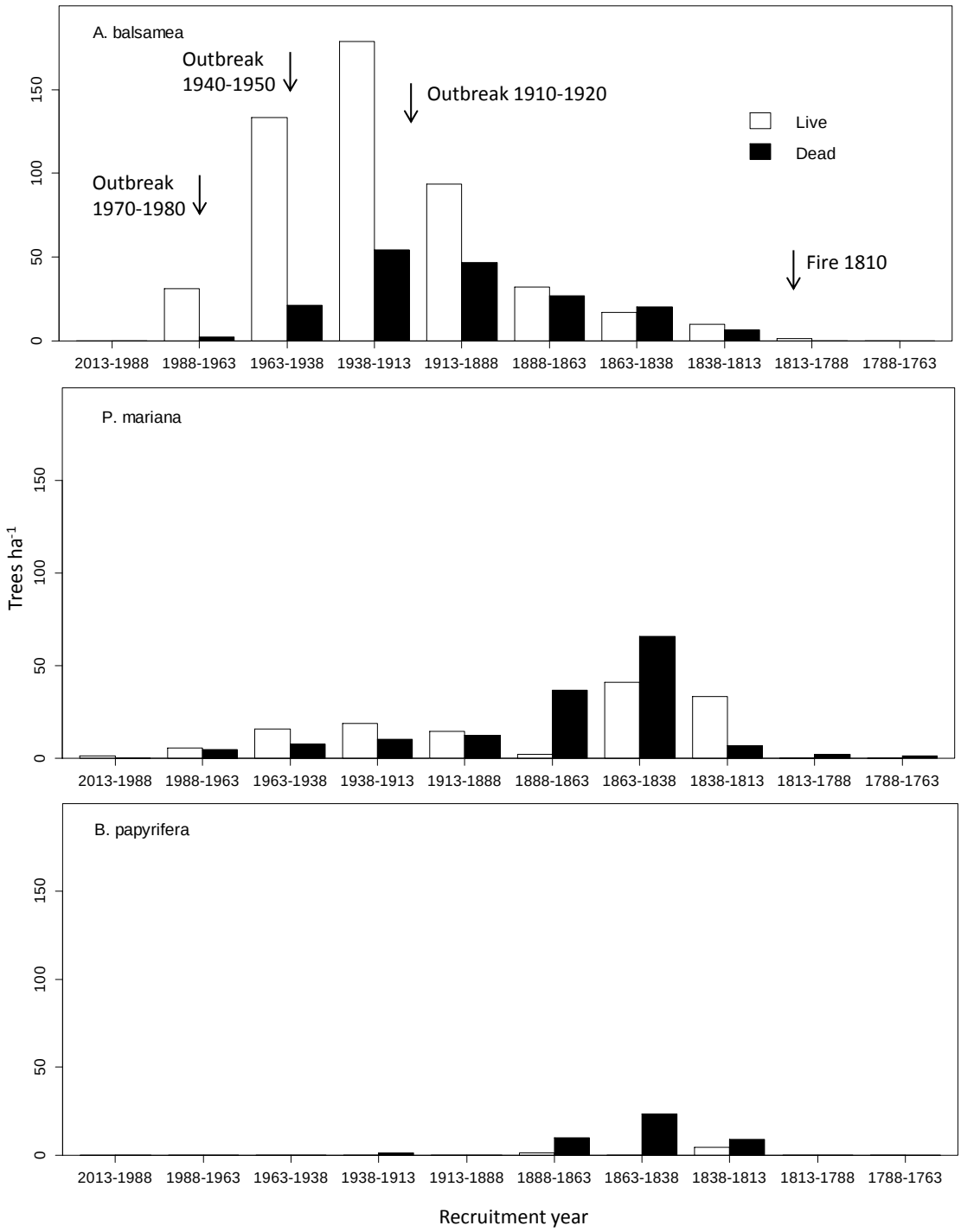

Fig. 9. Tree age distribution of *Abies balsamea*, *Picea mariana* and *Betula papyrifera* in all nine sites combined, with timing of the past disturbances. Class break is 25 years.

3.4 Tree species composition in 2013 and 1975

The tree species composition in 2013 consisted of *A. balsamea*, *P. mariana* and *B. papyrifera* (Fig. 10). *A. balsamea* was the dominant and most abundant tree species in seven out of nine sites; average amount of it for the whole study area was 12.2 m^2 ha^{-1} (SD ± 4.3 m^2 ha^{-1}) (Fig. 11). Site 3 and site 8 had more *P. mariana* than *A. balsamea*, 15.2 m^2 ha^{-1} and 17.7 m^2 ha^{-1}, respectively (Appendix 2, Table 4). The average amount of *P. mariana* for the whole study area was 8.0 m^2 ha^{-1} (SD ± 5.4 m^2 ha^{-1}). *B. papyrifera* was present to a minor extent in just over half of the sites; it was most abundant in site 3 (1.6 m^2 ha^{-1}). The average amount of *B. papyrifera* for the whole study area was 0.5 m^2 ha^{-1} (SD ± 0.6 m^2 ha^{-1}).

This situation was somewhat different in the past: in 1975 the composition consisted of *A. balsamea*, *P. mariana* and *B. papyrifera*, the latter two in notably higher numbers than in the present state of the sites, and of *P. tremuloides* (Fig. 10). *P. mariana* was the dominant tree species in four sites: site 1 (10.0 m^2 ha^{-1} of *P. mariana*/7.9 m^2 ha^{-1} of *A. balsamea*), site 2 (9.0/8.9 m^2 ha^{-1}), site 7 (14.2/6.7 m^2 ha^{-1}) and site 8 (30.3/2.0 m^2 ha^{-1}). The average amount of *P. mariana* and *A. balsamea* was 12.8 m^2 ha^{-1} (SD ± 6.9 m^2 ha^{-1}) and 10.3 m^2 ha^{-1} (SD ± 4.6 m^2 ha^{-1}), respectively (Fig. 11). *B. papyrifera*, which was present in all of the sites in 1975, was most abundant in site 1 (4.9 m^2 ha^{-1}). The average amount of it was 1.7 m^2 ha^{-1} (SD ± 1.5 m^2 ha^{-1}) for the whole study area. In 1975, *P. tremuloides* was present in site 4 (3.2 m^2 ha^{-1}).

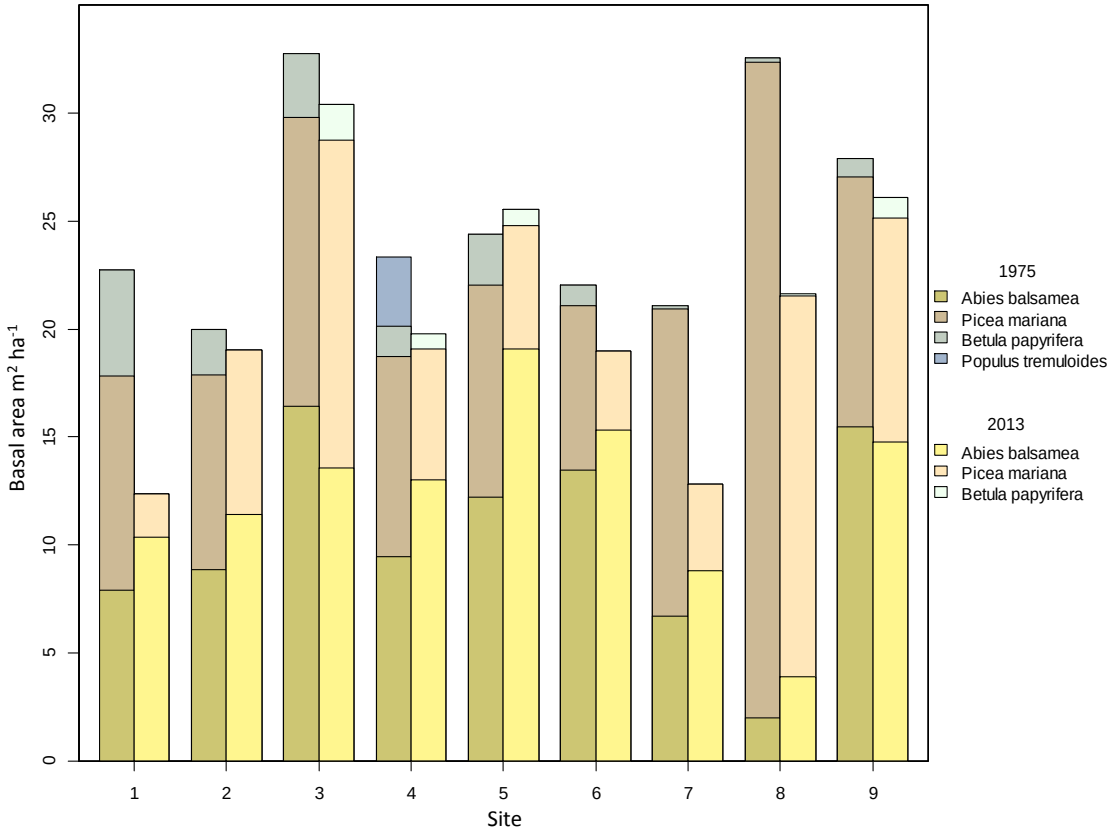

Fig. 10. Tree species composition in 1975 and 2013 per site.

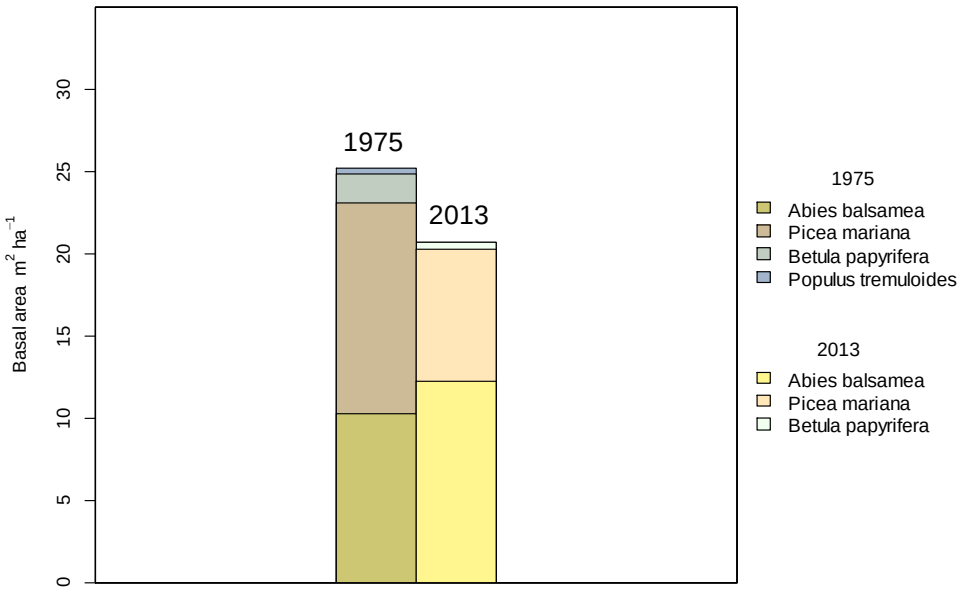

Fig. 11. Tree species composition in 1975 and 2013 for the whole study area.

3.5 The development of basal area

The development of total basal area from 1975 to 2013 was observed in each of the nine sites. Sites showed different types of development: for some of the sites basal area had dropped throughout the observation period, for some the total basal area had started to recover after a decline, and some sites had fairly stable development throughout the observation period (Fig. 12). In the years following the outbreak, the basal area dropped rather significantly in all sites. The basal area of the sites had plummeted from 1975 to present state in each of the sites.

The most dramatic decline was on site 1 during 1975-1999; the decline measured between the maximum value of 1975 basal area and the site's lowest year (1999) was 25.4 m^2 ha^{-1} (Fig. 12, Table 5). As a contrast, the basal area of site 2 showed almost no change at all after the drop following the outbreak, only falling slightly towards 2013 (Fig. 12). With the 1975 maximum value, the change was 10.5 m^2 ha^{-1} between 1975 and 2013 (Table 5). Site 3's and site 5's basal area seemed to be gradually recovering after a few falls during the observation period, whereas site 4's basal area was declining towards 2013 after a slow increase before 2002. Site 7's and site 8's basal area seemed to be declining almost throughout the observation period, site 7 declining 17 m^2 ha^{-1} from 1975 to 2013, and site 8 declining 19 m^2 ha^{-1} from 1975 to 2008.

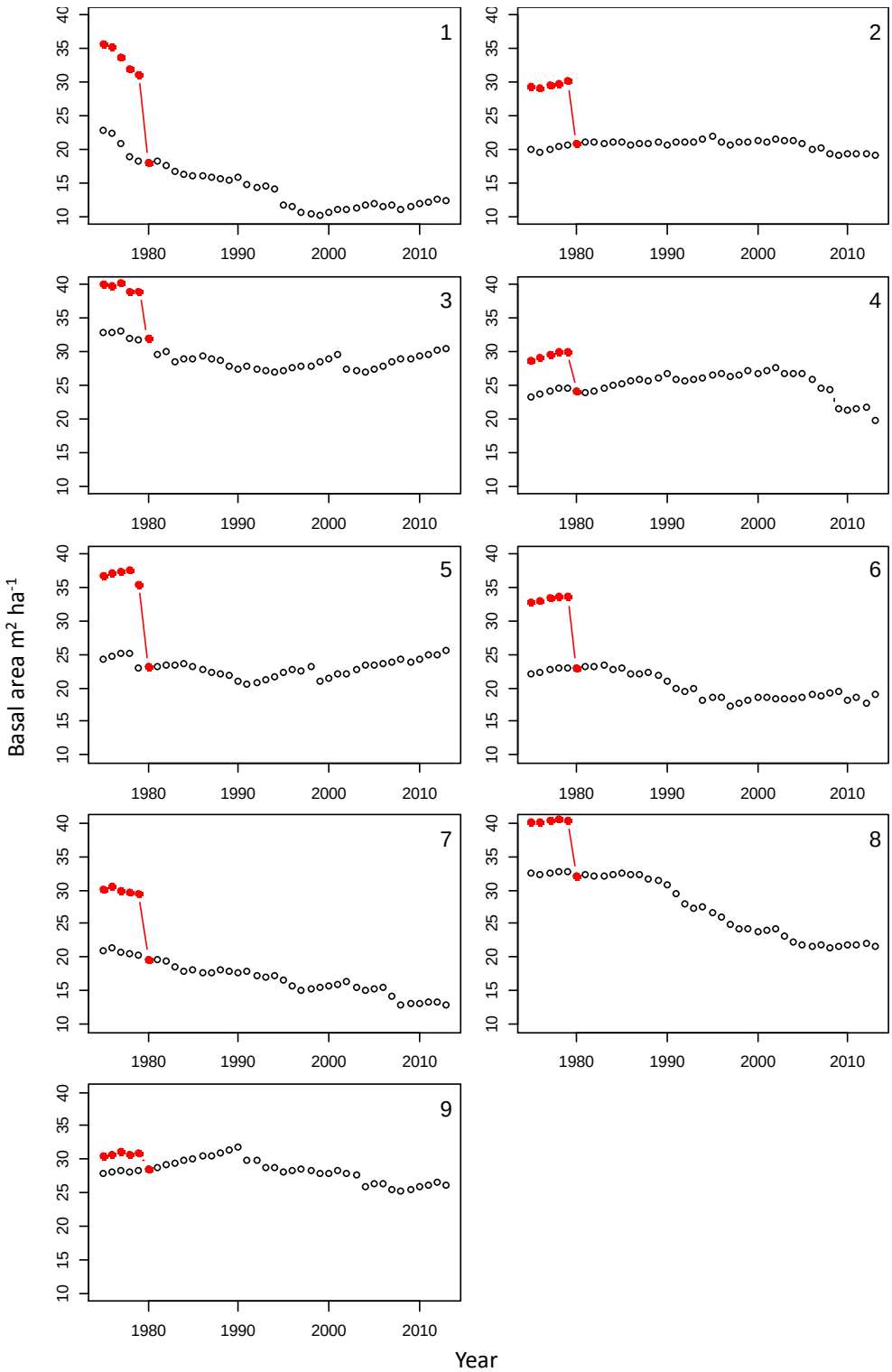

Fig. 12. The 1975-2013 development of total basal area for sites 1-9. Red circles present the estimated basal area of undated dead trees from decay classes 4 and 5, which were assumed to have died during the outbreak.

Table. 5. Basal area reduction between 1975 and the year of the lowest basal area per site. Minimum is the measured reduction of basal area with dated trees only and maximum is the estimated reduction of basal area with undated dead (decay classes 4 and 5) trees before 1980. BA = basal area, SD = standard deviation.

Site	Minimum (m^2 ha^{-1})	Maximum (m^2 ha^{-1})	Year of the lowest BA
1	12.5	25.4	1999
2	1.0	10.5	2009
3	5.9	13.1	2004
4	3.6	9.0	2013
5	3.9	16.3	1999
6	4.8	15.4	1997
7	8.2	17.4	2013
8	11.0	18.8	2013
9	2.7	5.3	2008
Average	6.0	14.6	
SD	3.6	5.6	

The average development of total basal area from 1975 to 2013 for the whole study area was gradual reduction, after somewhat steep decline in 1980 (Fig. 13). The average basal area was 33.8 m^2 ha^{-1} (SD ± 4.5 m^2 ha^{-1}) in 1975 and 20.7 m^2 ha^{-1} (SD ± 6.0 m^2 ha^{-1}) in 2013. The annual fluctuation of basal area seemed to be fairly uniform between the sites, as the standard deviation forms steady pattern of development around the mean values throughout the observation period (Fig. 13).

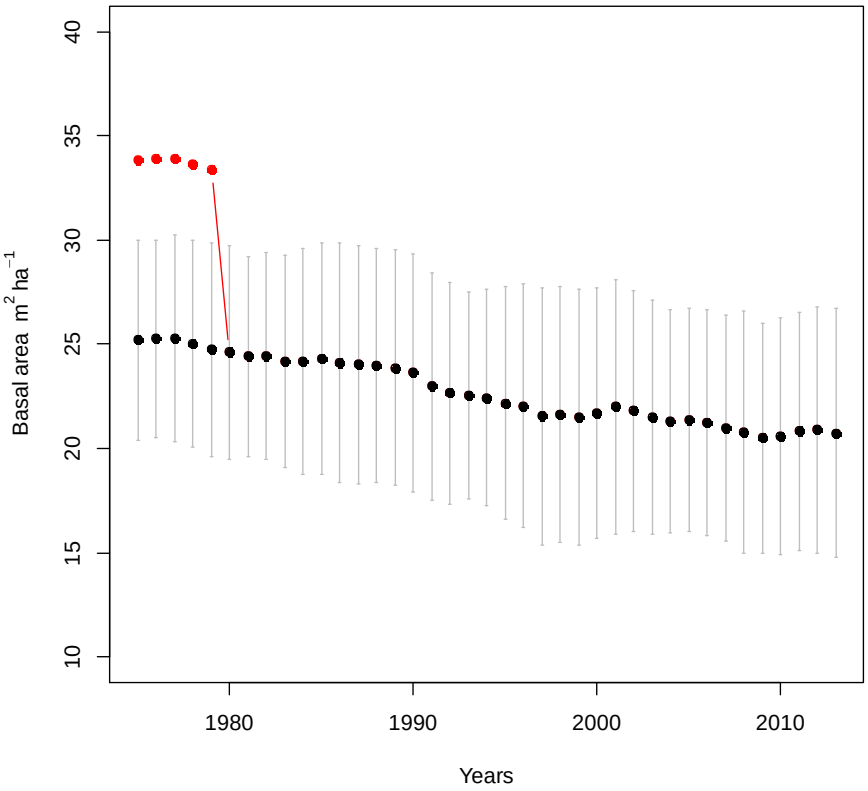

Fig. 13. The average development of total basal area for the whole study area, including average annual fluctuations (standard deviation).

The annual change of basal area of the past fifteen years (1999-2013) was examined to see if the development trend was positive or negative (Fig. 14). The trend was tested with a linear regression model. The slope of the fitted linear model appeared to be positive in four sites, but the annual changes were not significant (with p = 0.05 as the limit of statistical significance): site 3's slope was 0.032 (p = 0.445), site 5's 0.054 (p = 0.233), site 8's 0.018 (p = 0.511), and site 9's 0.028 (p = 0.454). Rest of the sites had negative slopes, but these were not significantly different from zero. Site 4 and site 7 had the steepest negative slope, with -0.087 (p = 0.123) and -0.027 (p = 0.409), respectively. Site 5 had the most positive slope, and site 2 (slope -0.018 p = 0.449), site 6 (slope -0.011, p = 0.780) and site 1 (-0.004, p = 0.841) regression lines had values close to zero, indicating steady, minor change development.

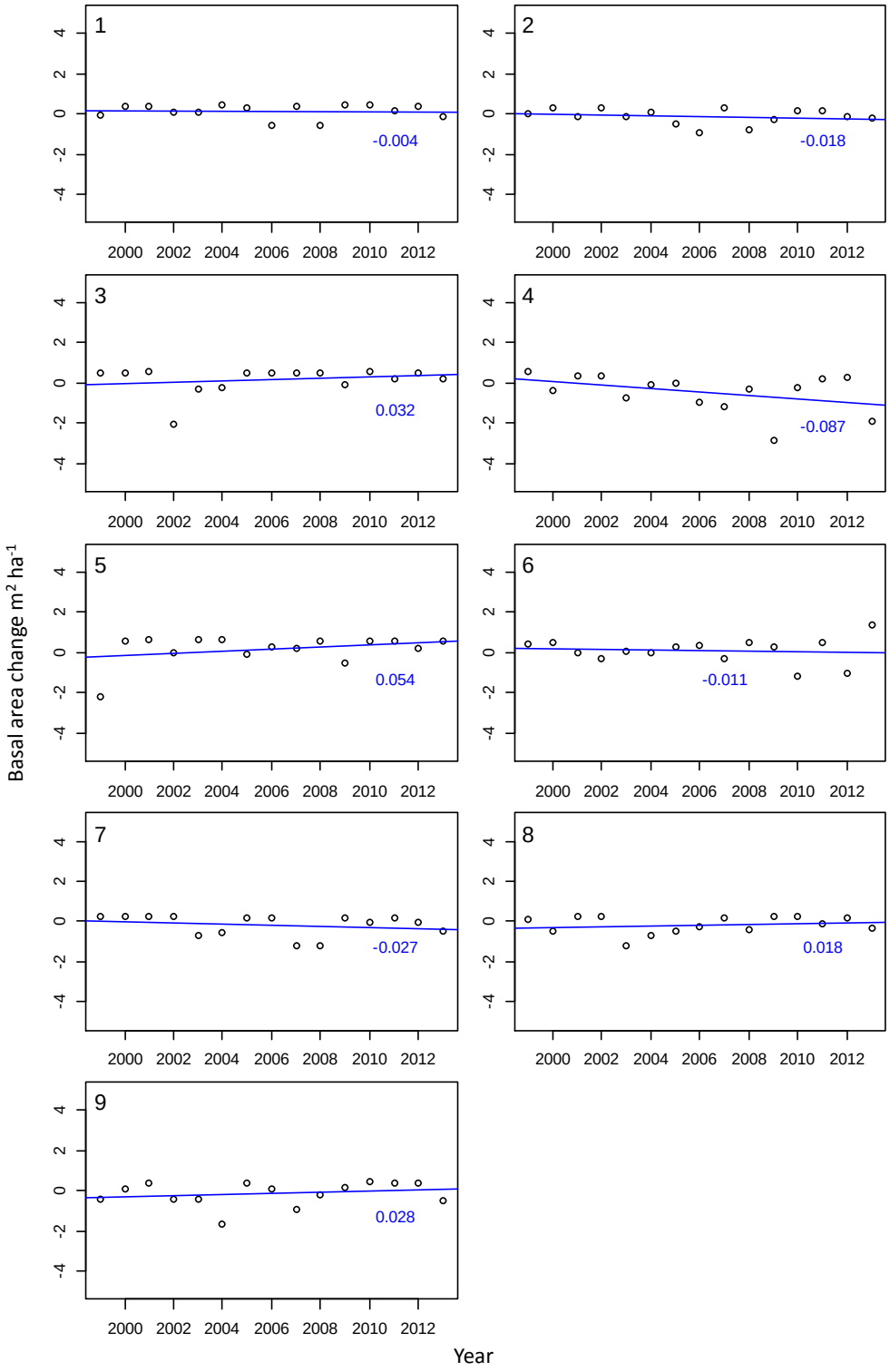

Fig. 14. The annual change of total basal area in 1999-2013 per site with fitted linear model. The blue text shows the slope of the linear model.

The average annual change of basal area for the whole study area indicated steady, minor change development with a slight negative slope for the past fifteen years (Fig. 15). The annual values seemed to fluctuate close to zero development, the largest

change was -0.30 m^2 ha^{-1} in 2003 and the smallest change was 0.067 m^2 ha^{-1} in 2005. The mean change for the whole observation period was -0.059 m^2 ha^{-1} (SD ± 0.2 m^2 ha^{-1}). The slope of the fitted linear model was -0.002 (p = 0.884) for the whole area, but it was not significantly different from zero.

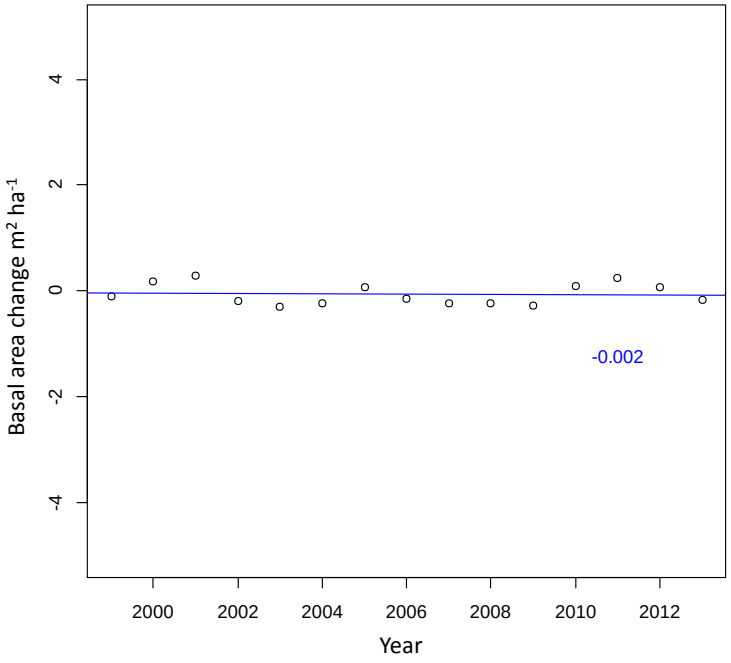

Fig. 15. The average annual change of total basal area in 1999-2013 with fitted linear model for the whole study area. The blue text shows the slope of the linear model.

4 DISCUSSION

4.1 Tree species composition, age and size structure

The aim of this research was to study the structure of natural *A. balsamea* dominated forest stands from 1975 to 2013. There are earlier studies describing post-outbreak stand and landscape development (Gauthier et al. 2010). However, the inter-annual pattern of this type of development has not been examined: whether the stands are recovering, in gradual decline, or following some theoretically expected trajectory of stand development, such as steady state (Bormann and Likens 1979, Fig. 1) or quasi-equilibrium (Caron et al. 2009), is uncertain. In this study, the problem of lack of permanent plot data was solved by using dendrochronological methods with tree-ring analyses, in which the forest characteristics were reconstructed at an annual resolution.

Tree species composition of the studied stands had clearly changed from the pre-episode to the current state. In 2013, *A. balsamea* dominated seven stands, and only two stands were dominated by *P. mariana* (Appendix 2, Table 4); on average for the whole study area, the amount of *A. balsamea* and *P. mariana* was 12.2 $m^2 ha^{-1}$ and 8.0 $m^2 ha^{-1}$, respectively. In 1975, *P. mariana* and *B. papyrifera* were much greater in volume than in the present stand state. *P. mariana* was the dominating tree species in four stands and few other stands had almost as much *P. mariana* as *A. balsamea*; on average, the amount of *A. balsamea* and *P. mariana* was 10.3 $m^2 ha^{-1}$ and 12.8 $m^2 ha^{-1}$, respectively. *B. papyrifera* seems to be disappearing from the tree species composition; in 2013, all the live measured *B. papyrifera* trees were over 100 years old and in the minority, whereas in 1975 *B. papyrifera* was present in greater numbers in all of the sites. In a study of stand renewal patterns in mixed forests of western Quebec, Bouchard et al. (2005) theorize that the outbreak in the late-1970s to early 1980s has accelerated or synchronized the mortality of non-host *B. papyrifera* trees, as environmental conditions have changed due to canopy disruption. It is also possible that certain amount of *B. papyrifera* trees were close to attaining senescence during and after the outbreak, which has made them more prone to environmental stresses caused by spruce budworm (Bouchard et al. 2005). Furthermore, previous studies have suggested that deciduous pioneer species are replaced by *A. balsamea* when the fire return interval is longer than the lifespan of the deciduous tree species (De Grandpré et al. 2000).

This studied increase in the abundance of conifer trees appears to be consistent with the post-fire succession pathways studied by Gauthier et al. (2010), where forest stands become dominated either by *A. balsamea* or *P. mariana* over time, as the importance of hardwood trees decreases. As present *P. mariana* trees were mostly over 125 years old, and lower canopy classes were dominated by *A. balsamea* (over 400 trees ha^{-1}), the change towards increasing dominance of *A. balsamea* appears likely. The subject of tree replacement patterns of *A. balsamea* and *P. mariana* in the boreal forests of Quebec has been widely studied previously, with contradictory results. According to several studies, *A. balsamea* dominance over *P. mariana* increases over time, and *A. balsamea* can be found abundant in late-successional forests where fire has not been present for long periods of time (De Grandpré et al. 2000, Bouchard et al. 2008). However, it seems that the probability of *P. mariana* being completely replaced by *A. balsamea* is extremely low, as the latter one is more susceptible for disturbances such as insect outbreaks (Pham et al. 2004, Gauthier et al. 2010). It also appears that in the mixed forest stands of both *A. balsamea* and *P. mariana* there seems to be reciprocal replacement of the species: *A. balsamea* replaces the gap made by *P. mariana*, and vice versa (Pham et al. 2004).

The influence of the past outbreaks in the North Shore appeared to have affected the current age structure as well. A majority of the live *A. balsamea* trees were in two age classes, 50-75 year old trees and 75-100 year old trees: the recruitment year is thus between 1938 and 1963 in the first age class and 1913 and 1938 in the second. Eastern Canada experienced two major spruce budworm outbreaks in the beginning of the 20th century, in 1910-20 and 1940-50 (Blais 1983); this might indicate that the present state *A. balsamea* trees are a result of those outbreaks. On average, the trees were of all age, which reflects the uneven-aged structure of old-growth forests (Oliver and Larson 1996). Mean age for live *A. balsamea, P. mariana* and *B. papyrifera* trees was 91 years (SD ± 32 years), 135 years (SD ± 48 years) and 180 years (SD ± 24 years), respectively. However, oldest live trees in the stands were *A. balsamea* trees. They belonged in the age class of 200-225 year old trees, meaning that their recruitment year was between 1788 and1813. According to Bouchard et al. (2008), the last large-scale forest fire in the study area was in 1810, and thus the age of the oldest trees is consistent with the timing of the forest fire, implying that this early-19th century fire was somewhat stand-

replacing. The recruitment year of the oldest live *B. papyrifera* trees (1813-1838) also implies that they are a result of post-fire succession.

The shape of the live tree diameter distribution for the whole study area was close to a reverse-J; live trees of smallest size classes (DBH < 18 cm) were the most abundant in all of the sites, and tree numbers usually dropped in the larger size classes. According to Boucher et al. (2003), about 70 % of the North Shore region's coniferous stands have currently an irregular or reverse-J diameter distribution (cited in De Grandpré et al. 2009). Reverse-J is often considered to be the traditional characteristic of natural old-growth forests (Oliver and Larson 1996), and also connected to forest stands that have undergone slow, post-disturbance stand establishment of long duration (McCarthy and Weetman 2006). However, there was some stand-to-stand variation in the shapes of studied diameter distributions. Five stands reflected the classical reverse-J fairly well, whereas two stands had diameter distributions closer to a rotated sigmoid, with a plateau or an increase in the mid-diameter distribution range. Two stands were something between a reverse-J and a rotated sigmoid. A number of studies from boreal forests of Fennoscandia have results of natural old-growth Norway spruce stands which mostly resemble the rotated sigmoid distribution (Linder et al. 1997, Kreutz et al. 2015). The rotated sigmoid distribution of live trees can be interpreted as a result of differential mortality rates: trees of different size have gone through the competition stage but have not yet reached the size-related mortality stage (Fraver et al. 2008, Kreutz et al. 2015).

The shape of the diameter distribution of dead trees differed from those of live trees: dead tree diameter distribution for the whole study area was closer to a rotated sigmoid. Dead trees were more abundant in the mid-sized diameter classes (DBH > 18 cm), but decreased towards the larger (DBH > 30 cm) size classes; this indicates that the outbreak of late-1970s to early 1980s has particularly caused mortality to mid-sized trees. Bergeron et al. (1995) found that trees in the larger size classes (DBH > 11 cm) are more prone to spruce budworm caused mortality than smaller trees. At the same time the outbreak has probably accelerated the growth of smaller understory trees, which partly explains the shape of the reverse-J diameter distribution of live trees; the outbreak of late-1970s to early 1980s has been studied to favor the abundant *A. balsamea* dominated sapling layer (Bouchard et al. 2005).

4.2 Basal area development

The examination of the development of total basal area showed apparent changes during the four decades from 1975 to 2013. The average stand development of total basal area for the whole study area was modest decline after a dramatic post-outbreak drop: the basal area was 33.8 m^2 ha^{-1} (SD ± 4.5 m^2 ha^{-1}) in 1975 and 20.7 m^2 ha^{-1} (SD ± 6.0 m^2 ha^{-1}) in 2013 (Fig. 13).

However, individual stands showed considerable difference in their development (Fig 12). The basal area had fallen throughout the observation period for three stands, two stands had fairly steady development over three decades and two stands showed recovery after a different degree of decline in basal area; two stands were something between these development courses. Stands reached their lowest point of basal area in various years, three stands during the 1990 decade, three stands during the twenty-first century and three stands in 2013. The basal area of the stands dominated by *P. mariana* and *P. mariana-A. balsamea* mixtures seemed to be affected by the outbreak similarly as *A. balsamea* dominated stands, although spruce budworm outbreak occurrences are connected with matured *A. balsamea* stands (Blais 1983). This is in line with the findings by Bouchard et al. (2006), suggesting that the outbreak of late-1970s to early 1980s has had a higher impact than earlier outbreaks on stands dominated by *P. mariana*.

The uncertainties in stand-level development were connected to the magnitude of the decline after the outbreak: if only the dated trees were calculated, biggest decline between 1975 and the stands' lowest year of basal area was over 12 m^2 ha^{-1} and the smallest one was 1 m^2 ha^{-1}. If the estimated basal area of undated dead trees was included, the decline could be described as dramatic: the biggest decline was over 25 m^2 ha^{-1} and the smallest one was 5.3 m^2 $ha^{-}1$. With undated trees, the growth depression was more pronounced in 1975-1980, which corresponds to the outbreak more clearly than with dated trees only. However, it was clear that the stands' current basal area had collapsed from the pre-episode level. Even with dated trees, only one of the studied stands' basal areas in 2013 had recovered to and over the 1975 level. With the estimated basal area, the basal area of each stand was lower than in the beginning of the observation period: most of the stands were 10-20 m^2 ha^{-1} behind from the 1975 level, on average 13 m^2 ha^{-1} (Appendix 1, Table 4). *A. balsamea* dominated stands have been

found to remain weakened for a number of years following the outbreak (Bouchard et al. 2005), but the fact that several stands of this study had not reached their lowest point of basal area until 2013 suggests that the amount of trees continue to decline furthermore in the future, with more than thirty years after the outbreak.

The annual change of basal area of the past fifteen years (1999-2013) was examined to assess the growth trend and the development state of the forest structure. Furthermore, uncertainties related to wood decomposition were smaller on these recent trajectories. There appeared to be no trend in the annual changes ($p = 0.05$). The growth was positive in four stands, two stands had almost zero (negative) development, and three sites had negative development; however, none of these slope coefficients differed significantly from zero ($p > 0.05$ in all cases). The average annual change of basal area was less than one square meters per hectare. On average for the whole study area, the annual change of basal area for the past fifteen years indicated steady, minor change development with a slight negative tendency (-0.002, $p = 0.884$), but without statistical significance.

In addition to the consequences of the past outbreak, the North Shore's forests are experiencing an on-going defoliation by spruce budworm (QMNR 2011, cited in Bouchard and Auger 2014). This was visible in the studied stands, as the majority of present *A. balsamea* trees (~ 500 trees ha^{-1}) had suffered from defoliation of needles up to 50 %, and some (~ 100 trees ha^{-1}) had suffered from even heavier defoliation; *P. mariana* trees had suffered slightly less, most of them less than 25 %. It can be assumed that the basal area of the stands will decrease even more in the future due to the defoliation; the studied stands can thus be regarded to be structurally in an unusual state. The post-disturbance development model of steady state and quasi-equilibrium suggests that forest stands which have experienced a disturbance will develop so that the biomass of the forest recovers to the pre-outbreak level and over it, through several different phases (Bormann and Likens 1979, Caron et al. 2009, Fig. 1). Although the model does not have any preset temporal unit and thus can be regarded more as a concept, the results of this study suggests that the studied stands are not following the expected post-disturbance development at these time scales of 30-years of observation.

The representativeness of the studied sites was slightly uncertain, as one of the criteria for the study area was that the sites should be accessible i.e. close to roads; due to this,

the sites were in an area that was being logged. The reason why these areas were left untouched was unclear: either they had some element that prevented the logging or the logging was performed after the study was made.

5 CONCLUSIONS

The aim of this study was to examine the post-disturbance structural change of natural *A. balsamea* dominated Canadian forest stands. The structural change was studied at an annual resolution, with a focus on stand basal area and species composition.

The tree species composition had changed from 1975 towards abundance of *A. balsamea*, with a decrease in the volume of *B. papyrifera* in 2013, and, apparently, a decline of *P. mariana* in the future. The current stand structure is possibly a result of past disturbances: the study area's last large-scale forest fire in the beginning of the nineteenth century, the spruce budworm outbreak in the late-1970s to early 1980, and two other spruce budworm outbreak episodes of Eastern Canada in the twentieth century.

Compared to theoretical models of old-growth forest development, the studied forest stands have reached a state where the basal area is yet to be recovered from the decline following the spruce budworm outbreak in the late-1970s to early 1980s. The annual change of basal area in the past fifteen years has been negative in over half of the studied sites, and as the new, on-going defoliation of spruce budworm – that already has heavily affected particularly *A. balsamea* – proceeds, the basal area of the forest stands might be expected to furthermore decline in the future.

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APPENDIX 1

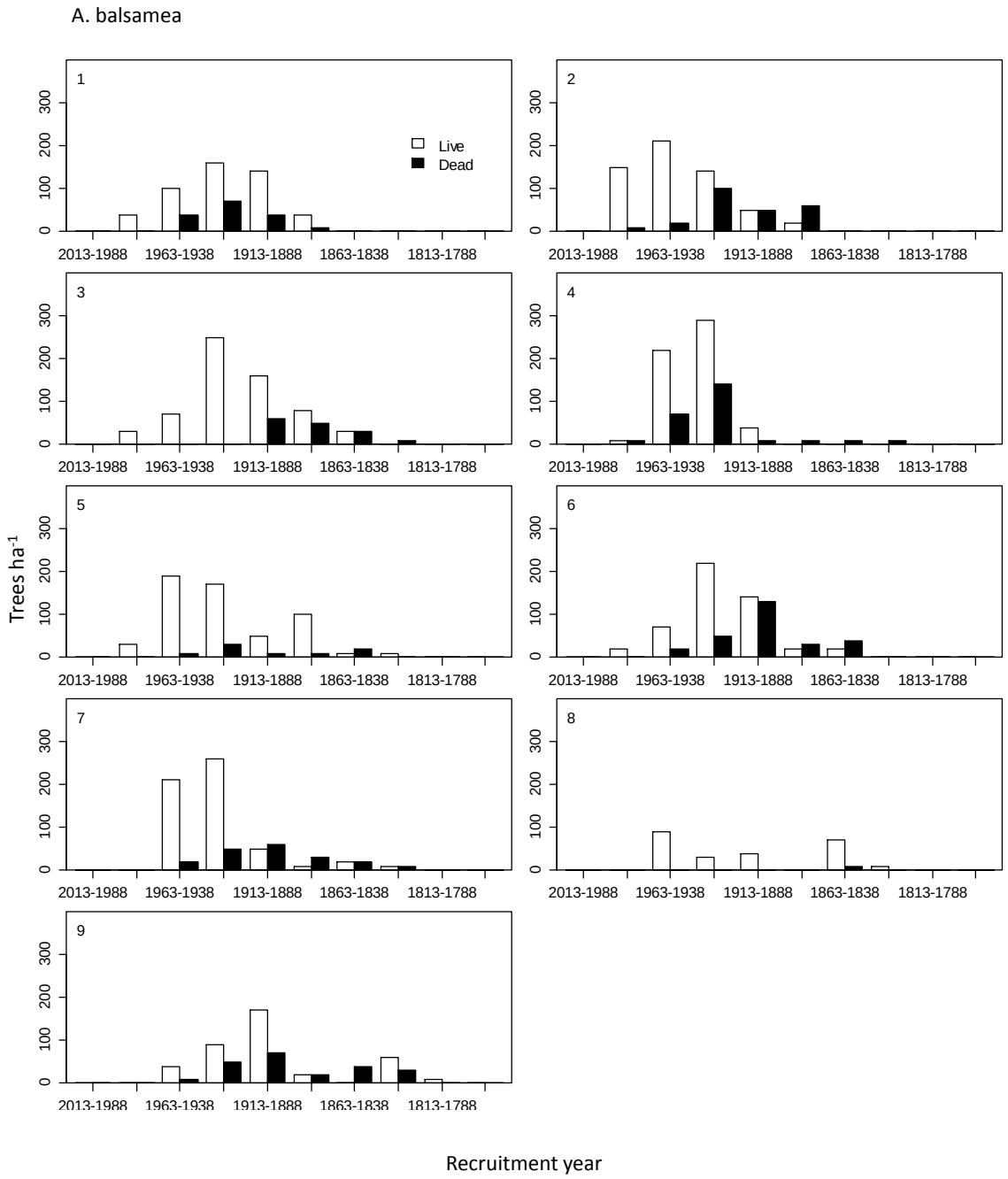

Fig 6. Tree age distribution for live and dead *Abies balsamea* per site. Class break is 25 years.

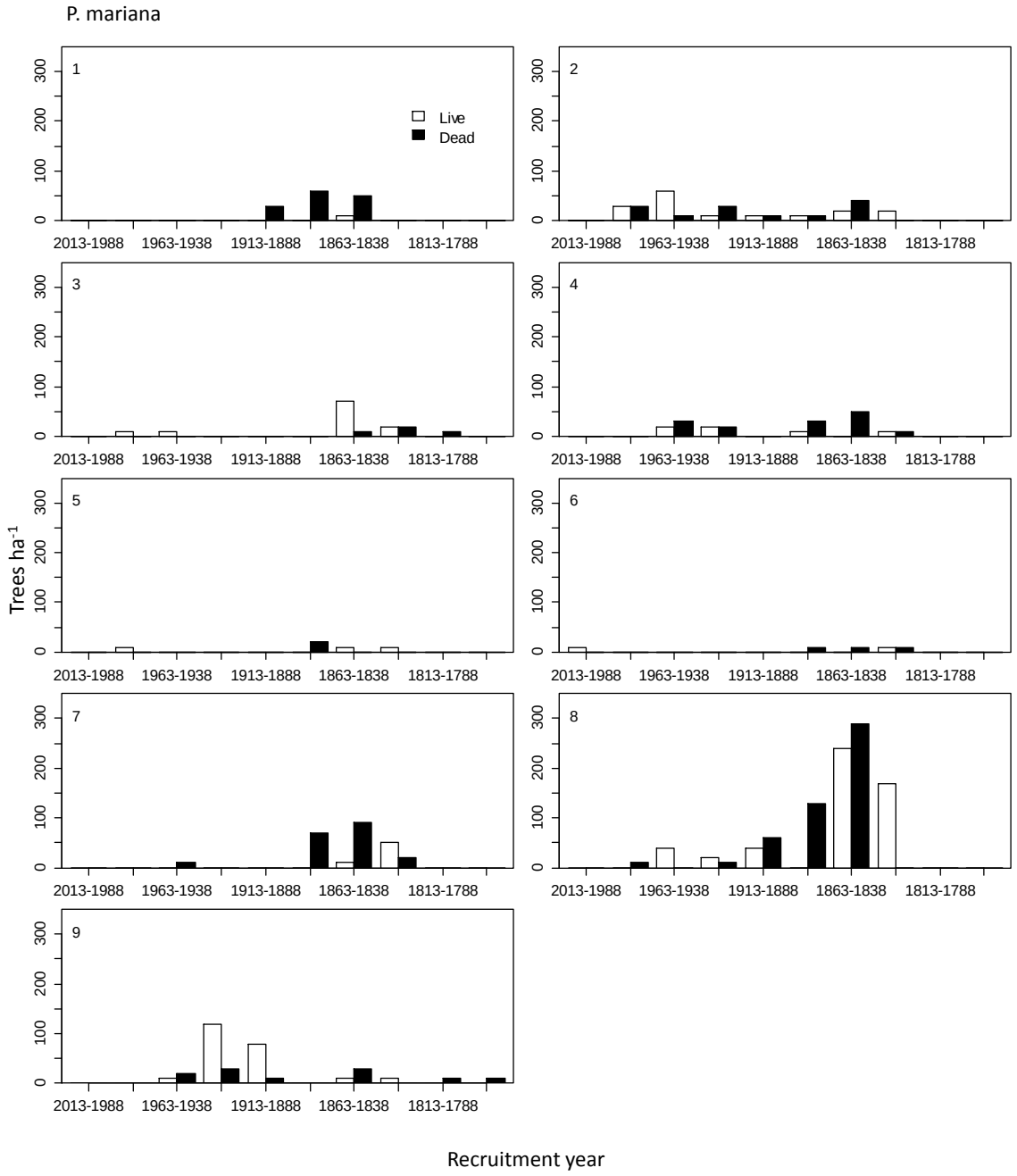

Fig 7. Tree age distribution for live and dead *Picea mariana* per site. Class break is 25 years.

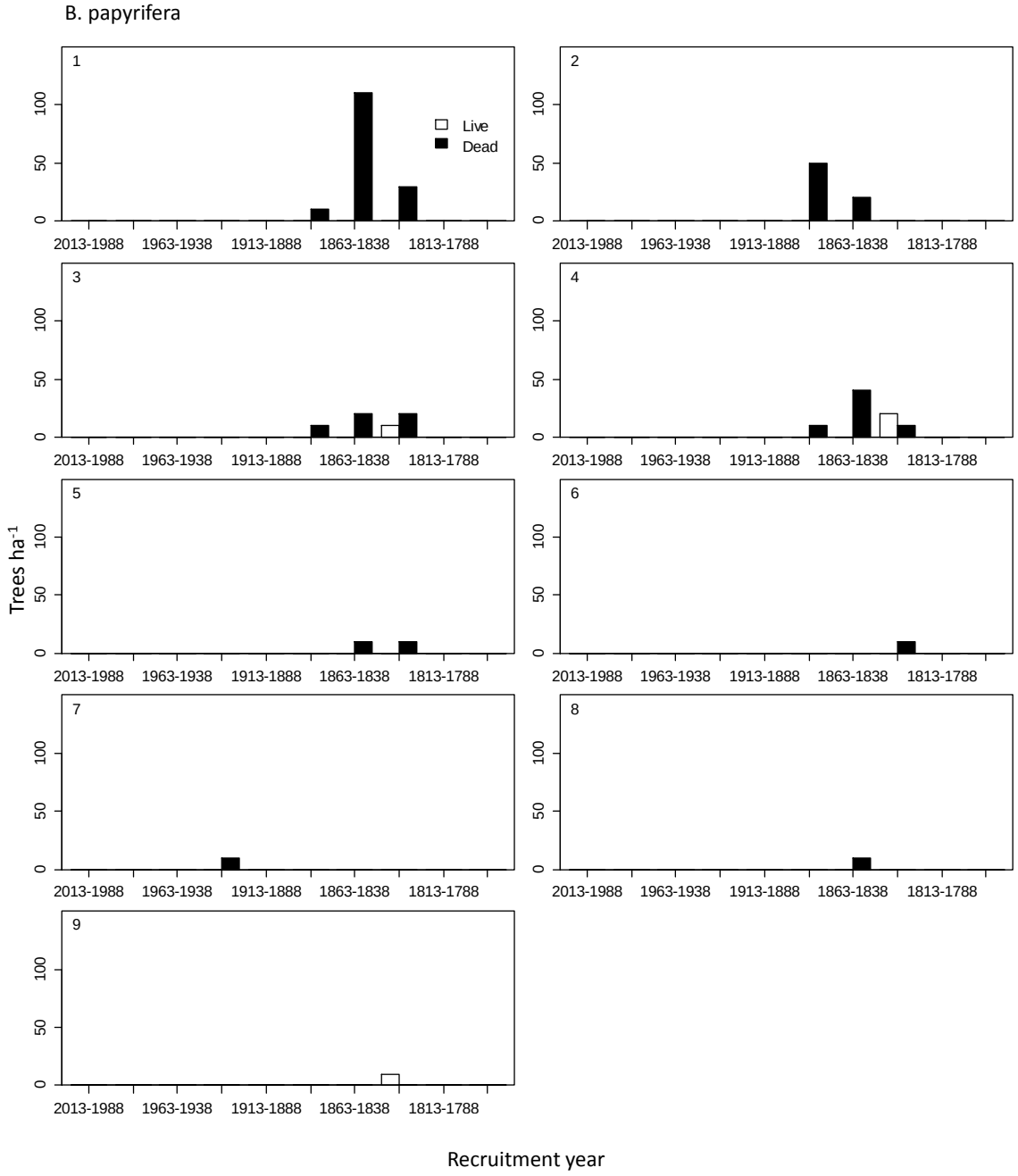

Fig. 8. Tree age distribution for live and dead *Betula papyrifera* per site. Class break is 25 years.

APPENDIX 2

Table 4. Total basal area per tree species per site in 1975 and 2013. Estimate includes the estimated basal area of dead, undated trees before 1980. Values are m^2 ha^{-1}. Aba = *Abies balsamea*, Pma = *Picea mariana*, Bpa = *Betula papyrifera*, Ptr = *Populus tremuloides*.

	1975					
Site	Total	Total + estimate	Aba	Pma	Bpa	Ptr
1	22.8	35.7	7.9	10.0	4.9	0.0
2	20.0	29.5	8.9	9.0	2.1	0.0
3	32.7	39.9	16.4	13.4	3.0	0.0
4	23.3	28.7	9.4	9.3	1.4	3.2
5	24.4	36.8	12.2	9.8	2.3	0.0
6	22.0	32.7	13.5	7.6	1.0	0.0
7	21.1	30.2	6.7	14.2	0.1	0.0
8	32.5	40.3	2.0	30.3	0.2	0.0
9	27.9	30.6	15.5	11.6	0.9	0.0
	2013					
Site	Total		Aba	Pma	Bpa	Ptr
1	12.4		10.4	2.0	0.0	0.0
2	19.0		11.4	7.6	0.0	0.0
3	30.4		13.6	15.2	1.6	0.0
4	19.8		13.0	6.0	0.7	0.0
5	25.6		19.1	5.7	0.8	0.0
6	19.0		15.3	3.6	0.0	0.0
7	12.8		8.8	4.0	0.0	0.0
8	21.6		3.9	17.7	0.1	0.0
9	26.1		14.8	10.4	1.0	0.0